

MONOECIOUS MORPHS IN
CROTON CALIFORNICUS (EUPHORBIACEAE)

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ABSTRACT

Croton californicus is reported to be a dioecious plant species. Monoecious morphs were observed in five populations in southern California. The prevalence of monoecious individuals was low with a total relative abundance of 2.2%. Female plants were more numerous than male plants in four of the five populations with a total male:female sex ratio of 0.90. Male plants were significantly larger than female plants for crown diameter and plant height while monoecious morphs did not differ significantly.

Croton californicus Muell. Arg. is a subshrub that inhabits sandy soils, dunes, and washes below 900 m in various plant communities of California, Arizona, and Baja California. It is reported to be a dioecious species (Webster 1993). Female plants bear small, whitish pistillate flowers with twice forked styles that resemble staminate flowers on male plants. The present study has noted monoecious morphs (Fig. 1) in several populations of southern California. It appears that *C. californicus* is currently in a diclinous condition other than dioecy proper. The purpose of this study was to document the occurrence and prevalence of monoecious individuals in several populations of *C. californicus*. Since most studies of dioecy have focused on temperate herbs (Ornduff 1981), the study of this subshrub should increase our incomplete understanding of sexual systems in woody plants and the evolution of plant breeding systems in general (Willson 1983).

METHODS

Measurements of *Croton californicus* were performed in five populations of southern California (Fig. 2). Populations at Loma Linda and California State University San Bernardino (CSUSB) were located in sandy soils of coastal sage scrub communities. The Loma Linda population was associated with *Encelia farinosa* Torrey & A. Gray, *Salvia mellifera* E. Greene, *Artemisia californica* Less., *Rhus trilobata* Torrey & A. Gray, *Keckiella antirrhinoides* (Benth.) Straw, and *Lepidospartum squamatum* (A. Gray) A. Gray. The CSUSB population was associated with *S. mellifera*, *A. californica*, *A. dracuncululus* L., *Eriogonum fasciculatum* Benth., and *Marrubium vul-*



FIG. 1. A monoecious morph of *Croton californicus* exhibiting (from left to right) a fruit, a pistillate flower, and a staminate flower adjacent to one another.

gare L. *Croton* populations at Rubidoux, San Bernardino, and Redlands were located in sandy soils of the Santa Ana River floodplain. The Rubidoux population was associated with *Baccharis salicifolia* (Ruiz Lopez & Pavon) Pers., *Urtica dioica* L. and *M. vulgare*. The San Bernardino population was associated with *B. salicifolia*, *L. squamatum*, *M. vulgare*, and the endangered *Eriastrum densifolium* ssp. *sanctorum* (Milliken) H. Mason. The Redlands population was associated with *Juniperus californica* Carriere, *E. densifolium* ssp. *sanctorum*, *E. fasciculatum*, *Eriodictyon trichocalyx* A. A. Heller, *Gutierrezia californica* (DC.) Torrey & A. Gray, *L. squamatum*, *Opuntia parryi* Engelm., *O. littoralis* (Engelm.) Cockerell, and *Yucca whipplei* Torrey.

The flowering season for *C. californicus* extends from March to October (Munz 1974). All flowering individuals in each population

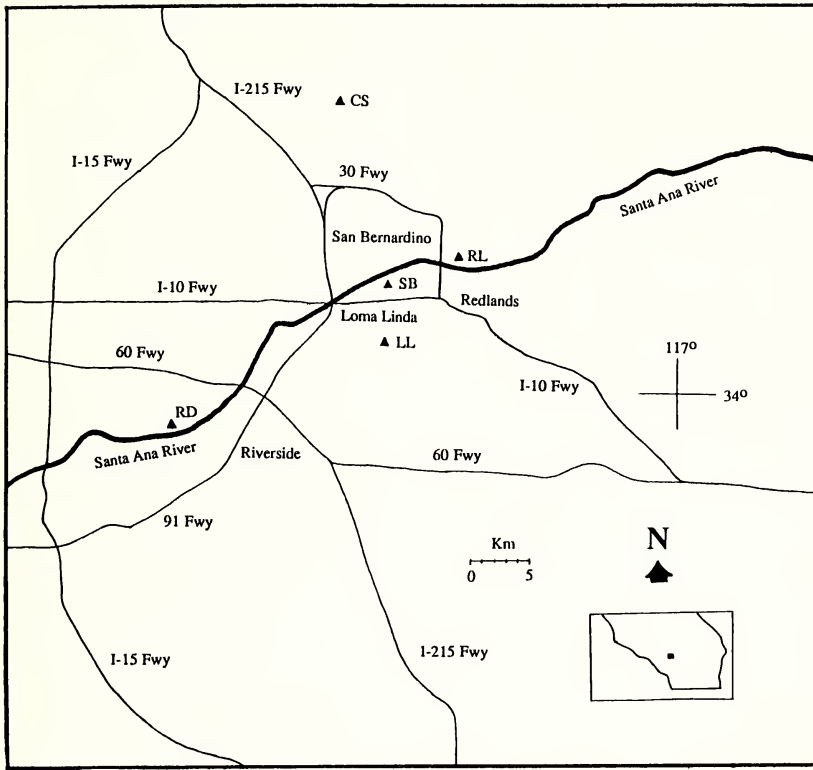


FIG. 2. Map of the study area. Study populations of *Croton californicus* are indicated by triangles. RD = Rubidoux; LL = Loma Linda; CS = California State University San Bernardino; SB = San Bernardino; RL = Redlands.

were examined near the end of the flowering season at Rubidoux, Loma Linda, and CSUSB on 3 October 1984, 7 October 1984, and 2 October 1985 respectively. Sexual condition was recorded and plant crown diameter, plant height, and leaf blade length were recorded for all the sexed plants or randomly recorded for many of the sexed plants. Sexual condition was determined by examining all of the flowers on a plant and by the presence or absence of fruits. Monoecious morphs were determined to be plants that bore both pistillate and staminate flowers. Leaf blade length was determined by sampling the largest leaf on each plant.

Samples of *Croton* populations in San Bernardino and Redlands were measured on 16 October 1991 and 23 October 1991 respectively. Plot sampling, using 1 m² quadrats, was performed in these two populations to determine population density, cover, and frequency as well as to record sexual condition and plant crown diameter. Cover was calculated from plant crown diameters. Although

TABLE 1. RELATIVE ABUNDANCE (%) FOR SEXUAL MORPHS OF *CROTON CALIFORNICUS* IN FIVE POPULATIONS OF SOUTHERN CALIFORNIA.

Population	Relative abundance						Male : female ratio
	Female		Male		Monoecious		
	n	%	n	%	n	%	
Rubidoux	121	55.5	95	43.6	2	0.9	0.79
Loma Linda	108	45.0	123	51.3	9	3.7	1.14
CSUSB	128	53.3	109	45.4	3	1.3	0.85
San Bernardino	55	53.9	43	42.2	4	3.9	0.78
Redlands	31	50.0	30	48.4	1	1.6	0.97
Total =	443	51.4	400	46.4	19	2.2	0.90

nonflowering plants and seedlings were also recorded, sexual condition could not be determined for these plants. Seedlings were designated as plants with crown diameters of less than 5 cm. Two hundred 1 m² quadrats were randomly sampled in each of these populations.

Statistical comparisons were made between sexual conditions and morphological data for all *Croton* populations using one-way ANOVA. Two-way ANOVA was also performed to analyze within and between population differences. Linear correlation was used to analyze the relationship of plant crown diameter with plant height.

RESULTS

Monoecious morphs of *Croton californicus* were present in all five of the study populations (Table 1). Relative abundance of monoecious morphs was low with a total relative abundance of 2.2% and values ranging from 0.9–3.9% for the different populations. Females were more numerous than males in all populations with the exception of Loma Linda. Male:female sex ratios ranged from 0.78–1.14 in the various populations with the total male:female ratio being 0.90.

Male plants of *C. californicus* were found to be larger when compared to female plants (Table 2). Male crown diameter was larger in all populations and significantly larger ($P < 0.05$) in three of the five populations. Male plant height was significantly higher ($P < 0.01$ or $P < 0.05$) than female plant height in two of the three populations measured. Totals for crown diameter and plant height also reflect that male plants were significantly larger ($P < 0.01$ or $P < 0.05$) than female plants. Monoecious morphs were not significantly different in size for crown diameter or plant height when compared to females or males in all populations. Crown diameter was correlated positively ($r = +0.775$, $+0.788$, and $+0.725$) with plant height for females, males, and monoecious morphs respec-

TABLE 2. MORPHOLOGICAL CHARACTERS (MEAN \pm SD) FOR SEXUAL MORPHS OF *CROTON CALIFORNICUS* IN FIVE POPULATIONS OF SOUTHERN CALIFORNIA. All units are in cm. Sample sizes are numbers in parentheses (n). RD = Rubidoux; LL = Loma Linda; CS = CSUSB; SB = San Bernardino; RL = Redlands. * = $P < 0.05$. ** = $P < 0.01$. There were significant differences ($P < 0.01$) among populations for crown diameter and plant height means.

Popula- tion	Morphological characters											
	Crown diameter					Plant height					Leaf blade length	
	Female	Male	Monoe- cious	Female	Male	Monoe- cious	Female	Male	Female	Male	Female	Male
RD	66.0 \pm 33.1* (121)	75.0 \pm 31.0* (95)	43.0 \pm 38.2 (2)	58.1 \pm 18.0** (121)	65.3 \pm 20.5** (95)	43.0 \pm 26.9 (2)	3.1 \pm 0.8 (121)	3.1 \pm 0.8 (95)	3.1 \pm 0.8 (121)	3.1 \pm 0.8 (95)	2.7 \pm 0.3 (2)	2.7 \pm 0.3 (2)
LL	39.8 \pm 25.9* (54)	52.5 \pm 29.0* (62)	60.4 \pm 25.1 (9)	48.1 \pm 16.2* (54)	54.1 \pm 16.4* (62)	52.9 \pm 12.5 (9)	2.7 \pm 0.7 (54)	2.6 \pm 0.7 (62)	2.7 \pm 0.7 (54)	2.6 \pm 0.7 (62)	2.4 \pm 0.6 (9)	2.4 \pm 0.6 (9)
CS	40.1 \pm 16.3 (62)	42.9 \pm 19.2 (57)	38.0 \pm 20.2 (3)	34.2 \pm 9.4 (62)	33.7 \pm 9.7 (57)	37.7 \pm 13.3 (3)	3.3 \pm 0.6 (62)	3.2 \pm 0.7 (57)	3.3 \pm 0.6 (62)	3.2 \pm 0.7 (57)	3.8 \pm 0.6 (3)	3.8 \pm 0.6 (3)
SB	28.6 \pm 14.3* (55)	36.6 \pm 16.6* (41)	45.3 \pm 31.6 (4)	—	—	—	—	—	—	—	—	—
RL	37.7 \pm 16.0 (31)	44.8 \pm 18.9 (30)	82.0 (1)	—	—	—	—	—	—	—	—	—
Total =	47.6 \pm 29.1** (323)	55.0 \pm 29.5** (285)	53.0 \pm 26.6 (19)	49.6 \pm 18.6* (237)	53.6 \pm 21.3* (214)	48.2 \pm 14.9 (14)	3.1 \pm 0.7 (237)	3.0 \pm 0.8 (214)	3.1 \pm 0.7 (237)	3.0 \pm 0.8 (214)	2.8 \pm 0.8 (14)	2.8 \pm 0.8 (14)

TABLE 3. DENSITY, COVER, AND FREQUENCY OF *CROTON CALIFORNICUS* IN TWO POPULATIONS OF SOUTHERN CALIFORNIA. Cover was calculated from plant crown diameters. K = number of 1 m² quadrats sampled.

Population	Phenological condition	Density (no./ha)	Cover (%)	Frequency (%)
San Bernardino (K = 200)	Flowering	5100	5.34	32.5
	Nonflowering	650	0.13	5.5
	Seedling	800	0.01	5.0
	Total =	6550	5.48	36.5
Redlands (K = 200)	Flowering	3100	5.07	24.0
	Nonflowering	350	0.14	3.5
	Seedling	100	<0.01	1.0
	Total =	3550	5.21	26.5

tively. There were significant interpopulational differences ($P < 0.01$) for crown diameter and plant height.

Density, cover, and frequency data for two populations of *C. californicus* is presented in Table 3. Density and frequency were higher in the San Bernardino population when compared to the Redlands population. Cover values are relatively close between populations with 5.48% in San Bernardino and 5.21% in Redlands. Both populations contained a considerable number of plants that were not flowering. Nonflowering plants and seedlings composed 22.1% and 12.7% of the plants sampled in the San Bernardino and Redlands populations respectively. Seedlings were more numerous than nonflowering plants in the San Bernardino population while the reverse was observed in the Redlands population. Many of the nonflowering plants in both populations were as large or larger than some of the flowering plants.

DISCUSSION

Although the frequency of monoecious morphs observed in this study was low, the occurrence of these morphs in populations of *Croton californicus* appears to be widespread in southern California. Many dioecious species are known to have populations with hermaphrodites at low frequencies (Charlesworth and Charlesworth 1978; Willson 1983; Bullock 1985) and there exist many intergrades between the various sexual systems of plants (Willson 1983; Bullock 1985). Bullock (1985) noted variable sex expression in some dioecious species of a tropical deciduous forest in Jalisco, Mexico, particularly in *Jatropha* and *Bernardia* of the Euphorbiaceae. Male plants vary in the tendency to produce a single female flower at the base of the inflorescence. The genus *Croton* is interesting for its diversity at this same locality: monoecy typifies most species, but the ratio of male to female flowers varies widely, and two species

consist of monoecious and female individuals; two species are dioecious (Bullock 1985; Tejada and Bullock 1988).

Unfortunately, the proportion of male to female flowers on monoecious plants was not quantified in this study. It was noted during data collection that on many monoecious individuals whole branches bearing pistillate or staminate racemes were situated on plants predominantly of the opposite sex. However, there were some monoecious plants that had several branches that were a mixture of both pistillate and staminate flowers. Often times pistillate and staminate flowers were situated alternate and adjacent (Fig. 1) to each other on the same raceme. One monoecious morph in the CSUSB population was noted to have one hermaphroditic flower as well as pistillate and staminate flowers. Three monoecious plants in the Loma Linda population were located within 1 m of each other. Close proximity of monoecious plants to one another has been recently noted by the author in four additional populations in December 1993. Although significant size differences of monoecious plants when compared to male or female plants were not detected in this study, this may be due to the small sample size ($n = 19$).

Vegetative parts of female and male *Croton* plants are morphologically identical which makes identification of the sexes impossible without flowers being present. This study observed size to be a secondary sex character in which males are larger than females. Most secondary sex characters of plants are subtle and usually are expressed in terms of growth, resource allocation, and timing or longevity (Richards 1986). Female biased sex ratios, as observed in this study, are rarer in nature than male biased sex ratios (Willson 1983; Richards 1986). The sex ratio in plant populations may not be equal due to microhabitat segregation by the different sexes (Handel 1983). There is some evidence in subdioecious species that females are relatively constant in their sex expression and it is the polleniferous plants which are variable (Heslop-Harrison 1957; Charlesworth and Charlesworth 1978). This may be true with *C. californicus* because when male and monoecious plants are added together, the male:female ratio is closer to 1.00.

Cover values of *C. californicus* in this study were similar to those found by Zembal and Kramer (1984). They found *C. californicus* closely associated with the endangered *Eriastrum densifolium* ssp. *sanctorum* in five out of six study populations. Cover values ranged from 0.3–5.8%, however, density values were lower than the current study. The immaturity of seedling plants in the present study did not allow many individuals in each population to be sexed. However, the nonflowering condition of the large number of plants in this study appears to be due to some factor other than immaturity. Possibly some of these plants were situated in drier locations and ceased flowering due to physiological stress.

Although monoecious individuals compose only a small fraction of a given population, their presence suggests that *C. californicus* may have an unusual breeding system. Three possibilities could explain the occurrence of the three sexual morphs. First, *C. californicus* may be a sequential hermaphroditic species that at any one time contains a small percentage of individuals undergoing sex reversal. If size determines when an individual switches sex, then we might expect the larger and most vigorous plants to be female (Willson 1983). This study observed that male plants were larger than female plants. Large male plants appeared to be healthy, vigorous, and not in any way senescent. There are several examples of dioecious species where the males are larger, taller, and/or more vigorous than the females (Willson 1983; Richards 1986). Longitudinal field studies are needed (Ornduff 1981) to monitor individual plants for one to several seasons to observe if sex reversal is occurring. Quantifying the number of pistillate and/or staminate flowers through time is necessary to reveal the femaleness or maleness of each individual plant.

Second, *C. californicus* may be in a subdioecious condition whereby some individuals exhibit phenotypic volatility for sex expression due to environmental influence. Phenotypic plasticity is well known (Willson 1983), and Heslop-Harrison (1957) cites many examples of plant intersexuality (a transformation from a normal condition of unisexuality to complete or partial bisexuality). Experiments are needed in which plants are subjected to changes in various environmental conditions such as light intensity, photoperiod, temperature, moisture, and pruning to see if sex expression is environmentally influenced (Heslop-Harrison 1957; Cleland and Ben-Tal 1981; Richards 1986). Also, experiments involving applications of various nutrients and plant growth substances such as nitrogen, auxin, ethylene, GA, cytokinins, and maleic hydrazide may reveal if there is any hormonal control of sex expression (Heslop-Harrison 1957; Cleland and Ben-Tal 1981; Richards 1986).

Third, *C. californicus* may be in a subdioecious condition whereby the three sexual morphs are genetically fixed. Genetic experiments, such as pollination between male and female plants, male and monoecious plants, monoecious and female plants, and monoecious and monoecious plants, are needed to reveal any relationship between genetics and sex expression.

The present study indicates that the second or third possibilities of a subdioecious sexual condition in *C. californicus* are more likely than the possibility of sequential hermaphroditism. Subdioecy represents a stage in the evolution from monoecy to dioecy or vice versa. It is likely that dioecy has evolved from monoecy on several occasions (Charlesworth and Charlesworth 1978; Ross 1982). Both

genotypic or phenotypic subdioecious conditions may reflect an evolutionary step for *C. californicus* from monoecy to dioecy.

ACKNOWLEDGMENTS

I thank Bill Khoury, Nalorn Sengamphan, Ernie Schwab, Gary Bradley and Norman Mitchell for their assistance with this study and manuscript.

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(Received 5 Apr 1994; accepted 20 Oct 1994)